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Causes of extinction of vertebrates during the Holocene of mainland Australia: arrival of the dingo, or human impact?

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Abstract: The arrival of the dingo in mainland Australia is believed to have caused the extinction of three native vertebrates: the thylacine, the Tasmanian devil and the Tasmanian native hen. The dingo is implicated in these extinctions because, while these three species disappeared during the late Holocene of mainland Australia in the presence of the dingo, they persisted in Tasmania in its absence. Moreover, the dingo might plausibly have competed with the thylacine and devil, and preyed on the native hen. However, another variable is similarly correlated with these extinctions: there is evidence for an increase in the human population on the mainland that gathered pace about 4000 years ago and was associated with innovations in hunting technology and more intensive use of resources. These changes may have combined to put increased hunting pressure on large vertebrates, and to reduce population size of many species that were hunted by people on the mainland. We suggest that these changes, which were quite dramatic on mainland Australia but were muted or absent in Tasmania, could have led to the mainland extinctions of the thylacine, devil and hen.

Key words: Dingo, vertebrate extinction, human impact, intensification, *Canis lupus dingo*, *Thylacinus Cynocephalus*, *Sarcophilus harrisii*, *Gallinula mortierii*, Holocene, Australia.

Introduction

The dingo *Canis lupus dingo* was introduced to Australia by about 3500 years ago (Gollan, 1984), and became established over the whole of the mainland. It did not reach Tasmania because rising sea levels had inundated Bass Strait about 6000 years earlier. The dingo is suspected of having caused the extinction of three vertebrates on the mainland – the thylacine (*Thylacinus cynocephalus*), the Tasmanian devil (*Sarcophilus harrisii*) and the Tasmanian native hen (*Gallinula mortierii*). It is implicated in these extinctions because, although these species disappeared from the mainland in the late Holocene, they survived in Tasmania in the absence of the dingo (Archer, 1974; Baird, 1991; Corbett, 1995). This correlation in space and time between the arrival of the dingo and extinctions is strong circumstantial evidence for an impact of the dingo, but it is persuasive only to the extent that no other possible causative factor was similarly correlated with the extinctions. The past 8000 years was a time of relatively stable and benign climatic conditions throughout Australia, and previous authors have found no change other than the arrival of the dingo that could plausibly be linked to extinctions of large vertebrates. However, there is evidence for quite dramatic changes in the human population of mainland Australia within the timeframe of the arrival of the dingo and subsequent extinctions. These changes include a variety of technological innovations, increases in population size and habitat range, and increasingly sedentary behaviour and more intensive resource utilization. They have been identified in many regions of mainland Australia and may represent a continent-wide phenomenon, but were muted or absent in Tasmania.

Changes in settlement patterns and resource use during the Holocene have been widely discussed in the literature of Australian prehistory, but prehistorians have not considered their relevance to late-Holocene extinctions of vertebrates, while ecologists are generally unaware of them. In this paper we develop an argument that these changes could have contributed to the mainland extinctions of the thylacine, devil and native hen. We begin by reviewing the mechanisms that have been proposed so far to link the dingo to extinctions of these species on the mainland.

Impacts of the dingo?

The thylacine was once widespread on the mainland of Australia, as well as New Guinea (Plane, 1976), but the most recent fossils

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outside of Tasmania are about 3000 years old (Archer, 1974). Both Archer (1974) and Corbett (1995) suggest that dingoes outcompeted thylacines. This view rests on the assumption that there was substantial overlap in the diets of dingoes and thylacines and that they therefore competed for food, a point that is generally accepted on the basis of the obvious morphological similarity of the two species. Corbett (1995) suggested that the dingo was the superior competitor because it had a more complex social organization than the thylacine. The dingo can hunt in integrated packs that cooperate to catch large prey and defend resources such as carcasses and water, while the thylacine may have been more solitary. This might have given the dingo a crucial advantage over the thylacine when resources were scarce, and made it a more efficient hunter of large macropods. Two other factors could have worked to the dingo's advantage: wild populations of the dingo may have enjoyed the demographic support of a semi-commensal relationship with humans, and the dingo might have introduced some disease to which the thylacine was susceptible (Corbett, 1995). The idea that the dingo displaced the thylacine on mainland Australia has been energetically disputed by Paddle (2000). His review of nineteenth-century observations of thylacine behaviour reveals a powerful and flexible predator that should have been able to resist competition from the dingo, which in any case (Paddle believes) did not become fully established in the wild until recent times. Paddle argues instead that the thylacine was driven to extinction on the mainland as a result of direct persecution by people. However, Archer (1974) had already discounted human impact as a factor in the extinction of the thylacine because of the difficulty of explaining why, given the long history of human occupation of Australia, people had not driven the thylacine to extinction on the mainland much earlier, and why they never did so in Tasmania.

The Tasmanian devil (*Sarcophilus harrisii*) had become extinct on the mainland by about 430 years ago (Archer and Baynes, 1972; Dawson, 1982). Devils are primarily feeders on carrion and depend largely on the carcasses of large-bodied species, such as wombats and the larger macropods, although they are also capable of capturing smaller species of live prey. Corbett (1995) argued that cooperative defence of carcasses by dingoes may have denied access to the primarily carrion-eating devils, who lack cooperative behaviour. The Tasmanian native hen was widespread on the mainland in the late Pleistocene, extending from the vicinity of the Burdekin River in north Queensland to western Victoria and eastern South Australia on the Murray River system (Baird, 1984; 1986; Mcnamara and Baird, 1991). There is one Holocene record, of 4670 years ago, in southwestern Victoria (Baird, 1991). The hen is a flightless ground-nesting bird that lives close to permanent water sources. Baird (1991) suggests that the range of the hen may have contracted during the drought conditions of the Last Glacial Maximum (about 20 000 years ago), and that it persisted within a reduced range until it was extirpated by the dingo.

These scenarios are plausible, but they contain some inconsistencies and on several points they are not well supported by evidence. First, there are significant morphological differences between the dingo and thylacine which suggest that niche overlap between the two species may have been overstated. The dingo has features typical of dietary generalists among canids, specifically a bicuspid talonid on the M_1 and well-developed hypocone on the M^1 (van Valkenburgh, 1991), and it eats a range of foods, including carrion, insects and seeds, as well as hunted mammals (Corbett, 1985). In contrast, the dentition of *Thylacinus* is that of a meat specialist, with minimal capacity for processing plants and invertebrates and without features that correlate with bone-cracking and scavenging in mammalian carnivores (Wroe, 2002; Wroe and Musser, 2001). Some features suggest that the thylacine took larger prey than the dingo. At a mean mass of 30 kg (Paddle, 2000), the thylacine was twice as heavy as the dingo. Its gape was wider than is typical in canids (Moeller, 1997), and wide gape is typically associated with the selection of larger prey (Savage, 1977; Wroe *et al.,* 1998). Moreover, energetic constraints have been shown to generally limit mammal predators above a mean body mass of 21.5 kg to relatively large prey (Carbone *et al*., 1999). Even allowing for the relatively low marsupial metabolic rate, the thylacine exceeded this threshold. Jones and Stoddart (1998) found that canine shape in the thylacine was also consistent with predation on large animals, but they concluded that it probably took relatively small prey, partly on the assumption that it did not hunt cooperatively, and partly because they observed a low incidence of fractured canines in thylacine skulls. However, Paddle (2000) has marshalled observational evidence suggesting that it was common for thylacines to hunt cooperatively, albeit in small groups. Further, the skulls that Jones and Stoddart (1998) examined may not have been representative, because most of them were collected in the nineteenth century. By then, the two largest potential native prey species of the thylacine in Tasmania, the emu and eastern grey kangaroo, were declining as the thylacine was pushed into increasingly marginal habitats (Paddle, 2000). Major shifts in prey selection toward smaller species have been documented for extant carnivores in response to human disturbance (Karanth and Sunquist, 1995). Thus, it is possible that rates of tooth breakage among nineteenth-century *Thylacinus* do not indicate the preferred size range of prey. We should also bear in mind that in widely distributed predators diet often varies greatly between habitats. For example, among African leopards (*Panthera pardus*), rain-forest populations typically concentrate on prey <5 kg in weight, a quarter the mean body mass of prey taken by savanna-based conspecifics (Ray and Sunquist, 2001). So, for the thylacine, diet in the restricted and distinct environments of Tasmania may have differed considerably from mainland populations.

Second, Corbett's (1995) argument that dingoes were capable of excluding thylacines from resources through cooperative behaviour is weakened by Paddle's (2000) conclusion that thylacines also hunted cooperatively. In any case, while it can form large packs, the dingo is often solitary or hunts in pairs (Marsack and Campbell, 1990; Thompson, 1992). In addition, the greater size of the thylacine could be expected to confer behavioural dominance over the dingo (Eaton, 1979; Palomares and Caro, 1999).

Third, there is a difficulty in explaining how it was that, if the dingo ultimately caused the extinction of the devil on mainland Australia, the two species coexisted for 3000 years. If the dingo's superior ability to defend resources was critical, one might expect the dingo to have had a greater impact on the devil than on the thylacine. This is because carcasses are more readily defended than live prey. Furthermore, being the smallest of the three predators, the devil would have been especially vulnerable to interference competition. Given that the dingo is anatomically better equipped than was the thylacine for scavenging and is known to feed on carrion, it is possible that ecological overlap between dingoes and devils was substantial, and in particular the dingoes' capacity for cracking bones may have meant that the remains of dingo kills provided relatively little food for devils. Moreover, although the devil is well adapted for scavenging large carcasses, it is also a successful predator of small and medium-sized vertebrates and so may also have overlapped with the dingo in its use of live prey.

Fourth, in one respect the arguments that the dingo caused the extinction of the thylacine and devil on the one hand and the hen on the other are in conflict. The idea that the dingo out competed the thylacine and devil rests on its ecological overlap with them, and the more ecological similarity that can be demonstrated the more plausible does competitive replacement seem. As argued above, the case for high ecological overlap between dingoes and thylacines, and dingoes and devils, is equivocal; but, if we assume

that the ecological similarities were substantial, this makes it puzzling that the hen was unable to coexist with the dingo, given that it had coexisted with both the thylacine and devil for many thousands of years beforehand.

These criticisms are certainly not fatal to the hypothesis that the dingo caused extinctions on mainland Australia. It is quite possible that the broad niche and behavioural versatility of the dingo made it competitively superior to both the thylacine and devil, as well as being an efficient predator of the hen. It is also possible that the impact of the dingo was amplified by its association with people. However, our general point is that the evidence linking the arrival of the dingo to the extinction of these three species is weak and in some respects inconsistent, and we should therefore be alert to other possibilities.

Intensification of human settlement on mainland Australia

The mid- to late-Holocene changes in the human population of Australia revealed by the archaeological record are often referred to as 'intensification', because they indicate, in one way or another, more intensive utilization of natural resources (Lourandos, 1997). Several distinct features of intensification that are especially relevant to consideration of ecological impact are summarized below.

Innovations in hunting technology

Between around 6000 and 4000 years ago, a wide range of more sophisticated stone tools appeared (Mulvaney and Kamminga, 1999; Flood, 1999). In particular, bifacial stone spear points appeared around this time, as did smaller-backed blades that were probably arranged in rows as barbs on hunting spears. Stone-tipped projectiles kill large animals more efficiently than do wholly organic spears and they are typically associated with hunting of large mammals (Boeda *et al.,* 1999; Ellis, 1997; Wroe *et al.,* 2002). In some areas, spearthrowers are known from the same period, although they may have originated earlier (Tacon and Brockwell, 1995; Walsh and Morwood 1999). Spear-throwers greatly increase the range and stopping power of traditional weapons (Hutchings and Bruchert, 1997), and the combination of spearthrowers with stone-pointed spears may have substantially increased the efficiency of large-mammal hunting.

Increased population density

Many regional analyses show increases in both the number of sites occupied by people and artifact discard rates at individual sites in the late Holocene, with significant increases typically beginning about 4000 years ago. Well-described regional examples can be found in reviews of archaeological trends in southern coastal New South Wales (Hughes and Lampert, 1982), Cape York Peninsula (David and Lourandos, 1997; Morwood, 1993), the Kimberley, Arnhem Land and central Queensland highlands (Morwood, 2002), southeastern Queensland (Morwood, 1987), the southeastern highlands (Flood *et al*., 1987) and western Victoria (Lourandos, 1983). Although such trends can be difficult to interpret, increases in both the number of sites in use and the intensity of use of individual sites (indicated by artifact discard rates) suggest increasing population size.

Expansion of habitat range and resource use

During the period that population size appeared to be increasing in long-occupied habitats, large-scale use of some hitherto unoccupied habitats began. These were generally habitats of low productivity. The sandy deserts of central and western Australia seem to have been unoccupied, or very sparsely occupied, prior to 5000 years ago, when use of the arid zone was restricted to the more favourable plateaux and gorge systems (Veth, 1989). Use of alpine and subalpine habitats (Flood *et al.*, 1987), rain forests (Cosgrove, 1996; David and Lourandos, 1997) and mallee woodlands (Ross, 1981) appears to be similarly recent.

Expansions in habitat range were paralleled by, and in some cases evidently dependent on, utilization of new types of resources. Veth (1989) and Edwards and O'Connell (1995) argue that the occupation of sandy deserts was made possible by the development of knowledge and technology for utilizing seed resources (Edwards and O'Connell, 1995; Veth, 1989). Although there is evidence for grinding and pounding stones much earlier (Field and Fullagar, 1998), standardized millstones for grinding seeds to make flour do not become widespread until after 5000 years ago. In central and north Queensland, the use of toxic plants such as cycads, that required extended treatment to make them edible, began around 3000 years ago (Cosgrove, 1996; David and Lourandos, 1997).

More sedentary behaviour

In some regions there is evidence for decreased range of movement and more permanent occupation in habitats that previously might have been used intermittently or seasonally. For example, in southwestern Victoria networks of channels were constructed to join lakes and swamps, evidently for the purpose of trapping fish and eels. Mound systems were built in the same area, providing permanent dry ground which would have allowed the continuous occupation of swampy habitats (Lourandos, 1983; 1997). These systems and others of comparable sophistication elsewhere in Australia are thought to be quite recent, and the major investment of time and effort required for their construction and maintenance suggests that they were at the centre of essentially permanent settlements. Very large and relatively recent middens on Cape York also indicate intensive and continuous occupation of particular coastal sites (David and Lourandos, 1998).

The topic of intensification has been rather controversial, and Australian prehistorians occasionally refer to 'the intensification debate'. Lourandos (1997) argues that intensification was a continent-wide process driven by an underlying social transformation, and that it was largely independent of environmental changes. Other authors lay more emphasis on regional variations in indicators of late-Holocene population change (Hiscock, 1986), and see many of the changes as being produced by simpler demographic processes or responses to environmental factors (Beaton, 1983; Bird and Frankel, 1991; Dodson *et al*., 1992; Rowland, 1999). However, there are difficulties in reconciling late-Holocene changes in resource use and population size as simple responses to changing environmental conditions. For much of the Holocene, rainfall was evidently higher than at present, and conditions were certainly more favourable than during the LGM, but a limited phase of aridification developed from around 3000 years ago (Kershaw, 1995). Late-Holocene increases in population size and expansion of resource use evidently coincided more closely with this arid phase than with the onset of humid conditions about 10 000 years ago. In particular, Ross (1981) points out that the expansion of human populations in the mallee cannot be explained by improvements in environmental conditions, because they occurred during a period of reducing rainfall, and in an earlier humid period there was no colonization; the same point can be made for the recent expansion into the arid zone.

Thus, despite some uncertainty over the interpretation of the late-Holocene archaeological record, there is a strong case for widespread changes in the pattern of resource use by people that may well have put increased pressure on Australian environments. The quite remarkable synchrony of parallel changes in many different parts of the continent suggests that impacts were very widespread. One sign that people might have been causing

environmental change in the late Holocene is that many pollen and charcoal records indicate substantial increases in landscape burning within the last 5000 years (Head, 1989; Kershaw *et al.,* 2002). This signal appears stronger than the rather dubious evidence for an increase in burning with the initial colonization of Australia (Bowman, 2000).

Impacts of intensification on vertebrates

Technical improvements in the hunting of large vertebrates, together with increased human population size (which may have been at least partly due to increased efficiency of hunting), might have resulted in reductions of population size for many hunted species. There are two types of evidence suggesting that there were such reductions. First, in some sites there was evidently a shift from concentration on the hunting of a few species of large mammals to use of a broader size range of species as intensification proceeded from about 5000 years ago. Examples are Bridgewater Cave in Victoria (Lourandos, 1983) and Gatton shelter in southeast Queensland (Morwood, 1986). This is what one might expect if increased exploitation of profitable (large-bodied) species brought about an increase in human population size, resulting in the depletion of those species and compensatory use of a broader range of less rewarding species. This is a common pattern in resource use by increasing populations of hunter-gatherers (Grayson, 2001). An alternative explanation for the trend is that increases in population size were due to broadening of the resource base as a result of development of techniques for using resources other than large vertebrates, so that large species made a progressively smaller proportional contribution to total prey capture. However, even if exploitation of large vertebrates did not drive change in the human population, an increase in population would result in higher rates of encounter of people with large prey and, probably, increased mortality rates from hunting for those prey. This would be especially likely if increased population size was associated with expansion into previously unoccupied habitats, as seems to have been generally true.

Second, there is evidence that some large mammal species which had been hunted by Aborigines experienced major increases in population size and geographic range when that hunting ceased within the last 200 years. Observations from many parts of Australia suggested that large kangaroos were uncommon when Europeans arrived (Barker and Caughley, 1992; Flannery, 1994). European settlers in the New England region initially found kangaroos to be 'very scarce', but kangaroo numbers then increased dramatically over a period of 40 or 50 years (Jarman and Johnson, 1977). Newsome (1975) describes similar increases from low numbers in red kangaroos (*Macropus rufus*) and wallaroos (*M. robustus*) in central and Western Australia following the establishment of European pastoralism. In New England, the increase in kangaroos did not correlate with changes in number of dingoes (Jarman and Johnson, 1977). Such increases have generally been attributed to changes in habitat, such as partial clearing of forests, the creation of short pastures and the provision of artificial water. However, they may also be consistent with a release from predation pressure following the breakdown of traditional patterns of resource use and reduction of population size of Aboriginal people.

Similar changes occurred for koalas (*Phascolarctos cinereus*) and tree kangaroos (*Dendrolagus*). Warneke (1978) notes that many early collectors had difficulty finding koalas in Victoria. A historical account from the lower Goulburn district (Parris, 1948) notes that koalas were initially unknown to European settlers, but began to appear in 1839 and were abundant by the 1860s. Parris believed that the increase of koalas was correlated with the decline of local Aborigines. Similar changes have been recorded for the Sydney region, where koalas expanded from the more dense forests and inaccessible sites into more open country (Strahan and Martin, 1982). Koalas in less densely wooded habitats and easier terrain were, presumably, especially exposed to hunting, and there are many observations suggesting that koalas were a favoured prey and were hunted with great skill (Martin and Handasyde, 1999). Similarly, early European collectors in north Queensland had difficulty finding tree kangaroos. According to Martin's (1996) account, Bennett's tree kangaroos (*D. bennettianus*) were restricted to high-altitude sites not visited by hunters, but with cessation of traditional use over the last 50 years they have extended their range into lowland forests and, very recently, into gallery forest along watercourses in savanna habitats (R. Martin, personal commication). Animals in such situations would have been very exposed to hunters in earlier times and, like koalas, tree kangaroos were favoured prey species. The examples of tree kangaroos and koalas provide stronger evidence that recent increases in population size were due to release from human predation, because for these species improvement of habitat following European settlement may not have been significant.

Mainland extinctions of Holocene vertebrates reconsidered

Could an increase in hunting pressure applied to vertebrates in the late Holocene have caused the extinction of the thylacine, Tasmanian devil and Tasmanian native hen? Hunting is most likely to cause extinction for species that have very small total population size or geographic range, and that are easily killed. This probably describes the Tasmanian native hen: the species is restricted to the proximity of permanent water, is flightless, but nests on dry ground so that eggs as well as adults are easy to harvest. It is difficult to imagine that it was not hunted. The sparse fossil record for this species suggests that by the Holocene it was restricted to wetland habitats in southern Victoria; the archaeological record demonstrates that humans increased their use of such habitats, and probably began to occupy them year-round, at about the same time that the hen became extinct (Lourandos, 1983; Baird, 1991).

Intensification might have contributed to the mainland extinctions of the thylacine and devil in two ways. First, both predators might have declined as a result of reduction in the abundance of their prey. If prey abundance declined to the point where the time and energy required to search for and capture prey exceeded the daily yield of energy from hunting, then predator populations would disappear. Extinction would be a possibility if there were no habitats in which prey populations were sufficiently dense to support viable predator populations. As described above, one striking trend in late-Holocene human populations on mainland Australia is expansion of habitat range, so that by about 3000 years ago all major habitat types were being exploited by people, perhaps for the first time in the history of human occupation of the continent. Continent-wide extinction of top predators as a result of reduced prey abundance therefore seems possible. This model provides a simple explanation of why the Tasmanian devil might have become extinct so much later than the thylacine. Larger and more specialized predators would be more sensitive to a decline in the population density of prey, because of greater individual energy requirements, lower initial abundance and lesser ability to compensate for rarity of preferred prey by switching to alternative prey. Therefore, one would predict that if abundance of vertebrate prey were gradually reduced during the late Holocene as a result of a steadily increasing human population, as seems likely, then the thylacine would have become extinct before the devil.

Second, extinction might have been caused by increased direct

hunting pressure. There is evidence from rock art in northern Australia that people hunted thylacines: paintings show thylacines being carried as prey, chased and (possibly) speared (Chaloupka, 1993, Guiler and Godard, 1998). A 6800-year-old human burial in western New South Wales is adorned by a necklace containing 178 devil incisors, representing at least 47 individuals, suggesting that this species may have been hunted quite heavily for ceremonial purposes (Flood, 1999). In historical times, Tasmanian Aboriginals hunted and ate thylacines (Plomley, 1966).

Tasmania

Holocene archaeology in Tasmania provides many contrasts with the mainland. In particular, there is no evidence for late-Holocene advances in technology. As Mulvaney and Kamminga (1999) put it: 'Because of their profound isolation, the Tasmanians missed out on innovations that became widespread across southeastern Australia.' Rather, there appears to have been a net decline in technological complexity during the Holocene, with the mid-Holocene loss of bone points (which had possibly been used to sew animal skins together to make capes) and cessation of fishing (Jones, 1995).

There was an expansion of settlement in Tasmania from about 4000 or 3000 years ago, consisting of increased use of the south and west coasts and the more heavily forested parts of the northern and western parts of the island, along with colonization of some near-shore islands. Lourandos (1997) suggests that this was due to a combination of the drier late-Holocene climate, which made sites that had previously been covered by very dense and wet forests more accessible and habitable, and use of fire to create more open conditions at such sites. Palynological records from Lake Selina in western Tasmania (Colhoun *et al.,* 1999) and Dublin bog in the north (Colhoun *et al.,* 1991), however, provide little evidence for increased landscape burning affecting distribution of vegetation communities in the late Holocene. The Tasmanian population had evidently expanded into and retreated from the wet portions of the north and west several times during the late Pleistocene in response to fluctuating environmental conditions (Holdaway and Porch, 1995), and the late-Holocene expansion may be best understood as a continuation of that pattern. There is little evidence that it was associated with increased intensity of resource use and at many sites there is a consistent reliance on the larger macropods for animal food. One site in northern Tasmania, Parmerpar Meethaner rock shelter, has a record of continuous occupation from 34 000 years ago through to European times. Artifact discard rates at this site vary substantially over time, being highest between about 18 000 and 10 000 years ago and lowest about 3000 years ago (Cosgrove, 1995). Discard rates increased slightly after 3000 years ago, but to nowhere near the levels of the late Pleistocene. Estimates of population density at the time of European settlement are about five times lower in northern Tasmania than in comparable environments of southern Victoria (Lourandos, 1997). This is consistent with an interpretation that late-Holocene increases in population inferred for Victoria did not occur in Tasmania. Barker and Caughley (1990) reviewed the distribution and abundance of the eastern grey kangaroo (*M. giganteus*) in Tasmania at the time of European arrival. A comparison of this study with a subsequent investigation, using very similar methods, of the eastern grey kangaroo in Victoria suggests that this animal was more abundant in Tasmania than in similar habitats in Victoria when Europeans arrived (Barker and Caughley, 1992). In Victoria, it subsequently increased, while in Tasmania it declined under European land use.

It appears therefore that in Tasmania changes in the human population were minor and were directly caused by changes in environment rather than by fundamental changes in use of terrestrial resources. Therefore, there is no reason to believe that the nature of human impacts on the Tasmanian environment changed in fundamental ways in the late Holocene.

Conclusions and implications

Earlier, we stressed that the only clear evidence implicating the dingo in the extinctions of the thylacine, Tasmanian devil and Tasmanian native hen is the coincidence between the arrival of the dingo and the disappearance of those species on the mainland, together with the absence of the dingo and their persistence in Tasmania. However, intensification of human settlement stands in the same relationship to these extinctions, and thus could be considered an equally well-supported hypothesis of cause. In certain respects, the intensification hypothesis may actually be more consistent with the chronology of extinctions. It accounts more readily for the early loss of the thylacine and later loss of the devil, and there is also a better-documented association between expansion of human settlement into the habitat of the native hen and the extinction of that species than there is for the spread of the dingo. These are rather fine points, however, and we believe that at present there is too little evidence to strongly favour one hypothesis over the other. Certainly, however, the prevailing view – that all available evidence points to the dingo as cause of the extinctions – should be revised. It might be worth adding that the arrival of the dingo, intensification and the mainland extinctions coincided approximately with a partial return to dry climatic conditions. It is unlikely that climatic change could have been a primary cause of the extinctions, because the drying was mild compared with what happened during the LGM, and affected Tasmania as well as the mainland. Nevertheless, it is at least possible that a reduction in rainfall around 3000 years ago exacerbated the impacts on native vertebrates of intensification and arrival of the dingo.

So far, we have presented the establishment of the dingo and intensification of human settlement as two distinct and separable processes. However, it is possible, and perhaps highly likely, that the effects on native vertebrates of the dingo and of intensification were synergistic. It is clear that the arrival of the dingo coincided with some aspects of intensification, and it is conceivable that it formed part of the cause of intensification. Dingoes and people hunted together and, in activities like the killing of tree kangaroos, they were a formidable partnership (Martin, 1996). Perhaps species that might have persisted in the face either of dingoes alone, or an increased human population alone, were unable to resist the pressures imposed by people who hunted with dingoes, or free-ranging dingoes maintained at high density by their association with people. Whether dingoes can be treated as an ecological factor separate from people depends on what proportion of the dingo population of late-Holocene Australia was associated with people or fully wild. Dingoes were certainly brought to Australia by people, and if most dingoes remained associated with people then their impacts on other species must be considered primarily in the light of their likely interaction with human hunters. If, on the other hand, dingoes established large populations in the wild soon after their release on mainland Australia, the impact of these populations could be regarded as independent of the human-dingo nexus.

Is it possible to distinguish the impacts on native vertebrates of establishment of the dingo and of intensification? Information on the history of association of dingoes and people will be essential for this, and could be derived from comparisons of the relative abundance of dingoes in sites inhabited by people with their abundance in comparable background sites. The issue could be further resolved by examining regional chronologies of intensification, establishment of the dingo and impacts on fauna. The arrival of

the dingo seems not to coincide exactly with all aspects of intensification: on present evidence, for example, the acquisition of stone spear points and spearthrowers preceded the arrival of the dingo, as did the occupation of habitats such as arid grasslands. This suggests that it might be possible to determine whether inferred changes in faunal abundance at particular sites correlate better with changes in human resource use and population size, or with the arrival of the dingo. This approach has not so far been taken in research on the prehistory and ecology of Holocene Australia.

Although the cause or causes of the extinctions of the thylacine, Tasmanian devil and Tasmanian native hen on mainland Australia remain unresolved, we believe the arguments developed in this paper do have some useful implications for our understanding of Australian ecosystems in the present day, and for their management. The most significant of these is that they help to build a case for the reintroduction of the Tasmanian devil to mainland Australia. The extinction of the thylacine and devil was a grievous loss to mainland ecosystems because it removed the continent's two largest marsupial predators. Although the thylacine is now (almost certainly) extinct in Tasmania as well as on the mainland, the devil remains abundant in habitats in Tasmania that are very similar to large areas of the southeastern mainland. Its re-establishment there would be a very significant step in the restoration of mammal communities on mainland Australia, and the ready availability of devils in Tasmania makes translocation to the mainland a practicable management option. One strong argument against this proposal might be that, if the extinction of the devil had been caused by the dingo, attempts to reintroduce it would be futile unless the dingo could first be removed from large areas of the mainland. The justification for reintroduction would be much stronger if we could show that the original extinction had been due to causes that no longer operate. This proposition is not proven, but in casting doubt on the belief that the dingo was responsible for the passing of the devil on mainland Australia we also throw a more favourable light on the idea that the devil could be brought back.

The more general implication concerns the way in which Australian ecologists interpret the history of human impact on Australian ecosystems. Such interpretations are usually based on ethnographic accounts of resource use by Aboriginal people in the recent past, which are projected backwards over the whole period that people are thought to have lived in Australia. Given that the size and distribution of the human population and, in particular, human impacts on the environment may have changed substantially in the relatively recent past, this approach is potentially very misleading. An example is the idea that traditional use of fire, which created a fine-scaled mosaic of patches at different stages of postfire succession, was critical to the maintenance of suitable habitat for medium-sized terrestrial herbivores (Johnson *et al*., 1989; Flannery, 1990; 1994). In Flannery's formulation of this model, firing of the landscape by Aboriginal people held the habitats of these species in a state which had formerly been maintained by the grazing and browsing pressure of the extinct marsupial megafauna. This idea is most powerful when applied to arid grasslands and shrublands, because many medium-sized mammals have recently become extinct from these habitats as traditional burning practices ceased. Yet the archaeological record suggests that occupation of many such habitats is only a few thousand years old. The timing of the extinction of the megafauna is still being debated, but it was certainly a Pleistocene event. One recent dating study places it at 46 000 years ago (Roberts *et al.*, 2001); other authors are unconvinced and suggest that around 30 000 years ago is a more probable date (Wroe and Field, 2001; Wroe *et al.,* 2002). This leaves a gap of at least 24 000 years between the megafauna extinctions and the establishment of landscape burning by people in the arid grasslands and shrublands, and rules out human use of fire as a critical factor in the persistence of medium-sized mammals in arid habitats.

A perspective from late-Holocene prehistory could also be important in interpreting environmental changes that followed the arrival of Europeans. Ecologists tend to assume that these were due to processes and forces driven or introduced by Europeans (the major exception to this being the view that relaxation of Aboriginal fire regimes could have produced significant responses in ecosystems). Perhaps, however, we should take more serious account of the possibility that Australian ecosystems were already undergoing quite rapid human-caused change during the few thousand years before Europeans came, and that what followed was due partly to the relaxation of Aboriginal impact and partly to the imposition of European impact, as well as to interactions between the two.

Note

After preparing this paper for publication, we became aware that some of the proposals in it had previously been raised by Kohen (1995). Readen should consult Kohen (1995) for an additional treatment of these issues; we apologize to Dr Kohen for not having cited his work in the body of the paper.

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